THE GENETIC IMPROVEMENT OF *EUCALYPTUS GLOBULUS* AND *E. NITENS* FOR SOLIDWOOD PRODUCTION

By

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DECLARATION

This thesis does not contain any material which has been accepted for a degree or diploma by the University or any other institution. To the best of my knowledge and belief this thesis contains no material previously published or written by another person except where due acknowledgment is made in the text of this thesis.

Matthew G. Hamilton

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STATEMENT OF CO-AUTHORSHIP

Where the candidate has co-authored a manuscript submitted for publication, the candidate undertook the research and major writing presented in this thesis. Co-authors oversaw the research projects and assisted with text preparation in a supervisory role.

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ABSTRACT

Eucalyptus globulus and *E. nitens* are among the most important plantation eucalypts in temperate regions of the world. Although pulpwood production is the principal focus of most forest growers, there is increasing interest in producing sawn-timber from *E. globulus* and *E. nitens* plantations. This thesis investigated breeding as a means of improving the solidwood characteristics of *E. globulus* and *E. nitens*.

Data relating to genetic variation in *E. nitens* was collated from the literature. However, only a small number of independent parameter estimates were available for solidwood traits. This was similarly the case in *E. globulus*.

In *E. globulus*, the lower stem, which represents a high proportion of total stem volume, was found to have the least favourable wood properties for kraft pulpwood and most solidwood applications. Subrace by height category interactions in bark thickness, basic density, decay and gross shrinkage indicated that differences among subraces were dependent on height in these traits.

The utility of measuring shrinkage in small wood samples (e.g.12-mm cores) as a cheap and non-destructive means of selecting against drying defects in sawn products was investigated. A number of methods of assessing shrinkage in samples were examined. Volume- and calliper-assessment of gross shrinkage were deemed the most promising assessment techniques based on genetic and practical considerations.

A strong genetic correlation between collapse and gross shrinkage in *E. nitens* wood samples indicated that most genetic variation in gross shrinkage was explained by collapse rather than normal shrinkage even when cores were dried at low temperature. In *E. globulus*, strong genetic correlations in gross shrinkage between drying treatments indicated that genotype by drying treatment interaction was of limited consequence over a wide range of drying conditions.

Relationships between pulpwood selection traits and sample shrinkage traits were investigated. Genetic correlations between basic density and gross shrinkage were generally negative (i.e. favourable) in both species. In contrast, the strength and direction of genetic correlations between growth and gross shrinkage varied widely

between and within studies. In *E. nitens*, the genetic correlation between predicted cellulose content and gross shrinkage was found to be positive (i.e. adverse) but not significantly different to zero.

Although significant genetic variation was detected in shrinkage traits, the efficacy of reducing drying-degrade in sawn boards by selecting trees according to sample shrinkage remains unclear. A small-scale *E. globulus* sawmilling study identified significant genetic variation in some board drying defects but did not find strong correlations between sample gross shrinkage and these defects. Furthermore, a very low intersite genetic correlation in sample gross shrinkage was observed in an *E. nitens* study.

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PUBLICATIONS FROM THESIS

Submitted publications

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Technical reports

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Hamilton MG, Greaves BL, Potts BM, Dutkowski GW (2007) Patterns of longitudinal within-tree variation in pulpwood and solidwood traits differ among *Eucalyptus globulus* genotypes. *Annals of Forest Science* **64**, 831–837. http://eprints.utas.edu.au/3393/

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Hamilton M, Joyce K, Williams D, Dutkowski G, Potts B (2008) Achievements in forest tree improvement in Australian and New Zealand. 9. Genetic improvement of *Eucalyptus nitens* in Australia. *Australian Forestry* **71**, 82-93. http://eprints.utas.edu.au/6788/

Hamilton MG, Raymond CA, Harwood CE, Potts BM (2009) Genetic variation in *Eucalyptus nitens* pulpwood and wood shrinkage traits. *Tree Genetics and Genomes* **5**, 307-316. http://eprints.utas.edu.au/7289/

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Hamilton M, Potts B, Greaves B, Dutkowski G (2010) Genetic correlations between pulpwood and solidwood selection and objective traits in *Eucalyptus globulus*. *Annals of Forest Science* **67**, Article 511. http://eprints.utas.edu.au/9835/

Hamilton MG, Dutkowski GW, Joyce KR, Potts BM (2011) Meta-analysis of racial variation in *Eucalyptus nitens* and *E. denticulata*. *New Zealand Journal of Forestry Science* **41**, 217-230. http://eprints.utas.edu.au/12425/

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CHAPTER 1

1. INTRODUCTION

1.1 *E. nitens* and *E. globulus*

1.1.1 Natural distribution

Eucalyptus globulus (Tasmanian Blue Gum) and *E. nitens* (Shining Gum) are closely related species (subgenus Symphyomyrtus, section Maidenaria, subsection Euryotae, series Globulares; Brooker 2000) native to south-eastern Australia (Table 1.1). The natural range of *E. globulus* extends from Tasmania to the adjacent costal regions of Victoria and includes the Bass Strait islands (Potts *et al.* 2004). In contrast, *E. nitens* has a scattered natural distribution that extends from the Central Highlands of Victoria to the Dorrigo area of New South Wales (Chippendale 1988; Boland *et al.* 1992).

Table 1.1 A comparison of natural distribution of *E. globulus* and *E. nitens* (Boland *et al.* 1992).

	E. globulus	*E. nitens*
Latitudinal range	38½ – 43½° S	30½ – 38° S
Altitudinal range	0 to 450 m	600 to 1600 m
Description of climate	Warm to cool, humid to sub-humid.	Cool to warm, humid to sub-humid.
Mean maximum temperature of the hottest month	20-23°C	21-26 °C
Mean minimum temperature of the coldest month	0 to 8°C	–5 to 2°C
Frosts	Around 5 to 40 or more each year.	Numerous and severe, with 50 to 150 each year.
Annual rainfall	600 to 1400 mm	750 to 1750 mm. Months with less than 50 mm are rare.

1.1.2 Distribution of plantations

There are large areas of *E. globulus* plantation in Australia (c. 349,796 ha in 2004), Chile (c. 232,000 ha in 2003), Portugal (c. 700,000 ha in 2002), Spain (c. 500,000 ha in 2002) and Uruguay (c. 200,000 ha in 2004; Potts *et al.* 2004).

Eucalyptus nitens is also a significant plantation species in temperate regions of the southern hemisphere, particularly in Australia (c. 160,000 ha in 2004) and Chile (c. 140,000 ha in 2004; INFOR 2004a). Worldwide, the area planted to both *E. globulus* and *E. nitens*, has expanded considerably over the past decade. The vast majority of these plantations are managed for the production of pulpwood (Tibbits *et al.* 1997a; INFOR 2004a; Potts *et al.* 2004).

Eucalyptus globulus has superior kraft pulping properties to *E. nitens* (Beadle *et al.* 1996; Tibbits *et al.* 1997; Kibblewhite *et al.* 2000) and there is some evidence from a laboratory based trial that *Chrysophtharta agricola* (a Chrysomelid beetle species) feeds on *E. nitens* foliage in preference to *E. globulus* (Lawrence *et al.* 2003). However, *E. nitens* is more cold hardy (Tibbits and Hodge 2003; INFOR 2004) and is less susceptible to Mycosphaerella leaf disease (Mohammed 2003) than *E. globulus*. *Eucalyptus nitens* is planted in preference to *E. globulus* where these factors are a substantial impediment to growth and/or survival.

1.2 Solidwood from *E. globulus* and *E. nitens* plantations

1.2.1 Introduction

Although pulpwood production remains the principal focus of most forest growers, researchers and wood processors, there is increasing interest in producing sawn-timber from *E. globulus* and *E. nitens* plantations for both structural and appearance applications (Neilsen and Pinkard 2000; McKenzie *et al.* 2003b; Bermúdez *et al.* 2004; FEA 2004; Gunns 2004; INFOR 2004b; McConnochie *et al.* 2004; Nutto and Vazquez 2004; Waugh 2004; Kube 2005b; Nolan *et al.* 2005). Currently, only a small volume of plantation grown *E. globulus* and *E. nitens* sawn-timber is produced and much of this is opportunistically recovered from pulp-logs rather than logs grown under solidwood silviculture (FEA 2004; Nutto and Vazquez 2004). Large scale *E. nitens* and *E. globulus* plantations managed under solidwood silviculture have been established in Australia (Neilsen and Pinkard 2000; FEA 2004; Gunns 2004) but few have reached harvestable age.

1.2.2 Structural products

Eucalypt sawn timber from native forest generally has superior strength properties to *Pinus radiata*, the most commonly utilised structural timber species in Australia, and attracts a premium price for use in strength critical applications (Nolan *et al.* 2005). However, the structural properties of unpruned plantation-grown *E. globulus* and *E. nitens* sawn timber are inferior to those of mature native forest timber due to their younger age and high frequency of knots (Waugh and Yang 1994; Yang and Waugh 1996b; Yang and Waugh 1996a; Nolan *et al.* 2005).

1.2.3 Appearance products

Appearance grade sawn timber demands a large premium over structural products of the same dimensions. However, sawmilling studies, and economic and financial modelling indicate that production of appearance-grade logs within acceptable rotation lengths requires the implementation of intensive solidwood silviculture (Gerrand *et al.* 1993; Candy and Gerrand 1997; Gerrand *et al.* 1997a; INFOR 2004a; Nolan *et al.* 2005). Such silviculture characteristically involves high initial stocking to control branch growth, thinning to maximise growth of individual stems with desirable form and branching characteristics, and pruning to produce knot-free timber (Gerrand *et al.* 1997b; Neilsen and Pinkard 2000; Nolan *et al.* 2005).

A number of sawmilling studies have shown that production of appearance-grade sawn products from *E. globulus* and *E. nitens* grown in appropriately managed plantations is possible (Waugh and Yang 1994; Moore *et al.* 1996; Reid and Washusen 2001; Washusen 2001; Nutto and Vazquez 2004; Washusen 2004; Waugh 2004). However, the recovery rates of dried product were highly variable among these studies. The identification and improvement of traits driving recovery will be necessary if a successful large-scale sawmilling industry is to develop.

1.2.4 Degrade in appearance grade products.

In sawmilling studies undertaken on logs from unpruned stands knots were the most common cause of downgrade in both structural and appearance products (McKimm *et al.* 1988; Thomson and Hanks 1990; Brennan *et al.* 1992; Waugh and Yang 1994; Yang and Waugh 1996b; Yang and Waugh 1996a; Washusen *et al.* 2000a; Washusen *et al.* 2000b; Yang *et al.* 2002; Washusen 2004). Drying degrade

is of particular concern to sawmillers and manufacturers of appearance-grade products as it has been shown to be a source of degrade in most sawmilling studies and is generally not exposed until substantial capital outlay and value adding has occurred (Chafe 1992; Taylor *et al.* 2003). Other sources of degrade in appearance-grade timber noted in *E. globulus* and *E. nitens* sawmilling trials include the presence of kino (i.e. dark reddish-coloured exudates; Bootle 1983), pith, stain, decay and growth stress (Thomson and Hanks 1990; Brennan *et al.* 1992; Washusen *et al.* 2000; Reid and Washusen 2001; Yang *et al.* 2002; McKenzie *et al.* 2003).

1.3 Drying degrade

Drying defects, such as cupping, face checking, internal checking, splitting and washboarding, are caused by within-board variation in shrinkage (Kauman 1964a; Bootle 1983; Chafe 1992; Vermaas 1995; Svensson and Martensson 1999; Taylor *et al.* 2003; Nolan *et al.* 2005).

1.3.1 Some definitions and explanations: Recoverable collapse, non-recoverable collapse, normal shrinkage, gross shrinkage and net shrinkage

Upon drying, wood shrinks as a result of a number of fundamentally different processes. Shrinkage caused by the buckling and flattening of cells is referred to as collapse (Figure 1.1; Chafe 1992). Conventional collapse occurs early in the drying process when tension forces, generated as free water is removed from cell cavities (i.e. lumens), exceed the strength of cell walls. It is most severe when wood is dried rapidly from the green condition (e.g. under high temperatures with low humidity and rapid air movement; Kauman 1964b; Chafe 1992; Ilic 1999; Nolan *et al.* 2003b) and has been observed to be negatively correlated with wood density (Chafe 1992; Ilic 1999).

Sawmillers use reconditioning (i.e. treatment with steam) to recover collapse after pre-drying. This component of collapse is referred to as ‘recoverable collapse’. However, collapse-induced fractures (e.g. checks and splits) remain after reconditioning and are sometimes exacerbated by it (Nolan *et al.* 2003b; Taylor *et al.* 2003). Furthermore, excessive and non-recoverable collapse is sometimes observed. Such collapse is often attributed to the presence of tension

wood, a form of reaction wood thought to develop as a means of reorienting stems (Chafe 1992; Washusen and Evans 2001b; Washusen and Ilic 2001; Waugh 2004; Nolan *et al.* 2005). However, some authors have suggested that, "much of the distortion (collapse) which takes place in the drying of tension wood can [in fact] be attributed to greater shrinkage of the cell wall (Wardrop and Dadswell 1955)" rather than 'conventional collapse' as outlined above. The effect of tension wood on the drying properties of *E. globulus* has been extensively studied (Washusen *et al.* 2001; Washusen and Evans 2001a; Washusen and Ilic 2001; Washusen 2002; Washusen *et al.* 2002). However, little research has been undertaken in *E. nitens*, possibly reflecting a belief that tension wood explains less of the drying defects observed in that species.

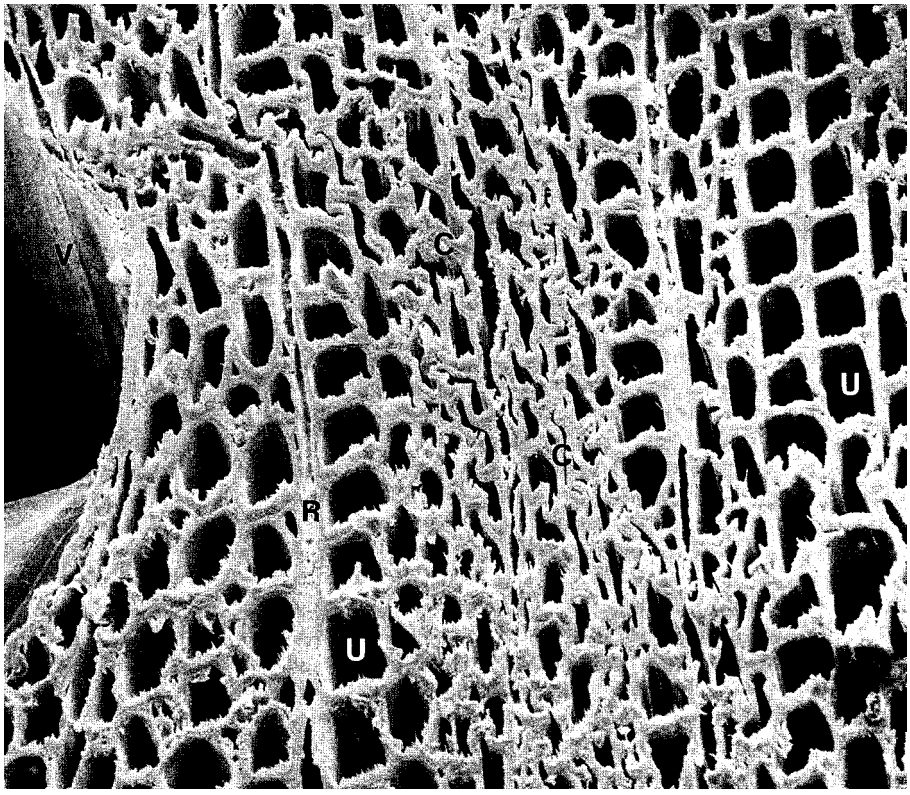

Figure 1.1 Scanning electron micrograph of a cross section of wood of *E. regnans* showing a radially-oriented band of collapsed fibres (C), uncollapsed fibres (U), a vessel (V) and rays (R). Image from Chafe (1992).

Normal shrinkage refers to a reduction in the thickness of cell walls that occurs as bound water is removed from them. It generally occurs late in the drying process once most or all free water has been removed from cell cavities (i.e. below the fibre saturation point; Chafe 1992; Babiak and Kudela 1995). If normal shrinkage in the

cell wall were homogeneous, normal shrinkage observed in the external dimensions of wood would be independent of basic density because the dimensions of the cell cavities would change in proportion to shrinkage in the cell walls (refer to Kelsey 1963). However, there is some empirical evidence to suggest that normal shrinkage is positively correlated with basic density in eucalypts (Washusen *et al.* 2001).

Wood absorbs and loses moisture depending on the relative humidity of the surrounding environment (i.e. it is a hydroscopic material). Just as wood shrinks as it loses moisture below a moisture content at or near the fibre saturation point, it swells as it gains moisture up to the fibre saturation point. The propensity of wood to shrink and swell below the fibre saturation point (i.e. its dimensional stability) is generally expressed as unit shrinkage. Unit shrinkage can be defined as the percentage change in a piece of timbers dimensions following a moisture content change of one percent (Kingston and Risdon 1961; Winandy 1994; Nolan *et al.* 2003a).

Gross shrinkage is observed in a piece of wood after drying but prior to reconditioning and is composed of normal shrinkage, recoverable collapse and non-recoverable collapse. Net shrinkage is observed after reconditioning and is composed of normal shrinkage and non-recoverable collapse.

1.3.2 How does drying degrade manifest itself?

Cupping, face checking, internal checking, splitting and washboarding are forms of drying degrade observed in eucalypt sawn timber.

1.3.2.1 Cupping

Cupping is curvature across the grain of a board, which causes it to be concave on one side and convex on the other (Bootle 1983). Cupping is more prevalent in backsawn than quartersawn boards (Figure 1.2) and is primarily explained by differences in shrinkage between the radial and tangential axes (i.e. shrinkage anisotropy; Winandy 1994; Vermaas 1995; Svensson and Martensson 1999).

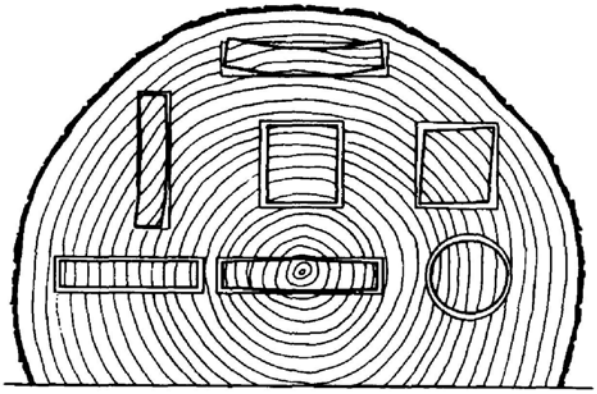

Figure 1.2 The effects of shrinkage anisotropy on the shape of sawn products. Note the cupped backsawn board (top) and uncupped quartersawn board (bottom left). Image from Winandy (1994).

1.3.2.2 Checking

Checking is a common cause of degrade in plantation grown *E. nitens* and *E. globulus* appearance grade sawn timber (McKimm *et al.* 1988; Waugh and Yang 1994; Lausberg *et al.* 1995; Washusen *et al.* 2000a; Reid and Washusen 2001; McKenzie *et al.* 2003b). Checks are radially-oriented cracks in timber that do not extend from one surface of a board to the other (Bootle 1983; Chafe 1992). A distinction is generally made between surface checks (alternatively known as face checks; Figure 1.3) and internal checks (i.e. checks that do not extend to a board face; Figure 1.4). However, internal checks can reveal themselves as raised grain on the surface of finished products or manifest themselves as surface checks when timber is sawn or machined (Taylor *et al.* 2003). As internal checks are not always identified until late in the drying or manufacturing process they can be particularly costly and are a common cause of customer complaints to Australian hardwood timber mills (Taylor *et al.* 2003).

Check-inducing drying stresses can develop in a board as a result of shrinkage anisotropy (Svensson and Martensson 1999), variation in collapse between latewood and earlywood (Kauman 1964a; Chafe 1992), variation in shrinkage between sapwood, heartwood and the sapwood/heartwood transition zone (Kauman 1964b; Lausberg *et al.* 1995), the presence of other defects (e.g. knots; Brennan *et al.* 1992) and moisture gradients within boards during drying (Taylor *et al.* 2003; Nolan *et al.* 2005). In extreme circumstances, such drying stresses can produce cracks that extend from one surface of a board to another (i.e. splits; Brennan *et al.* 1992).

Figure 1.3 Surface checks on a backsawn *E. nitens* board

Figure 1.4 Internal checking exposed at the end of a backsawn *E. nitens* board

1.3.2.3 Washboarding

After pre-drying (Nolan *et al.* 2003b), quartersawn boards are often observed to have a corrugated surface (Figure 1.5), a phenomenon informally described as washboarding or ring-collapse. Washboarding is caused by variation in collapse between latewood and earlywood. There is a tendency for washboarding to occur instead of internal checking in thin quartersawn boards (Chafe 1992).

Figure 1.5 Washboarding in *E. globulus* 12 x 12 mm pith-to-bark wood samples after drying at 105°C for 24 hours.

1.3.2.4 Technological, silvicultural and genetic solutions to drying degrade

Saw-millers can minimise the impact of drying degrade in sawn products by:

- changing sawing methodology (e.g. quarter sawing relatively thin boards; Bootle 1983; Haslett 1988a; Vermaas 1995; Taylor *et al.* 2003; Nolan *et al.* 2005),
- producing different products (e.g. structural-grade rather than appearance-grade sawn timber; Nolan *et al.* 2005),
- using mild and controlled pre-drying regimes to minimise collapse (Vermaas 1995; Nolan *et al.* 2003a; Nolan *et al.* 2003b),

- reconditioning timber after pre-drying to recover collapse (Chafe 1992; Nolan *et al.* 2003a; Nolan *et al.* 2003b; Taylor *et al.* 2003),
- planing away mild cupping, surface checks or washboarding after final-drying (Bekele 1995; Svensson and Martensson 2002; Ilic *et al.* 2003), and
- concealing degrade in final products (e.g. using fillers; Taylor *et al.* 2003).

In addition to these technological approaches, modified silviculture to minimise tension wood formation (Nutto and Vazquez 2004; Waugh 2004; Washusen *et al.* 2005) and breeding (Arnold *et al.* 2004; Kube and Raymond 2005) are being investigated as a means of reducing drying degrade in plantation-grown timber.

1.4 Breeding *E. globulus* and *E. nitens* for sawn-timber production

1.4.1 Economic benefits though breeding

Tree breeders aim to maximise the aggregate economic benefit to the forest grower and/or processor (i.e. the target enterprise) of genetic gains made in biological traits. Genetic gain in a biological trait can be broadly defined as the difference in the aggregate genotypic value (refer to Falconer 1986) for that trait between an 'improved' clone, family or population and its base population (i.e. the original 'unimproved' population). Tree breeders achieve genetic gain by exploiting genetic variation in a trait through the selection, crossing, testing and/or deployment of superior genotypes.

The aggregate economic benefit of genetic gain in one or more biological trait/s can be estimated if economic weights (i.e. the economic benefit of a one unit improvement of the trait/s) are known or assumed. Tree breeders generally judge the merit of genotypes according to their genotypic value for multiple traits and the economic weight of each of these traits (i.e. by using an index; Hazel 1943; Schneeberger *et al.* 1992; Apiolaza and Garrick 2001).

1.4.2 Breeding objectives

A breeding objective is a combination of biological traits, herein referred to as objective traits, which tree growers and/or processors wish to improve (Ponzoni and Newman 1989; Borralho *et al.* 1993; Greaves *et al.* 1997a; Apiolaza and Garrick 2001). Theoretically, "decisions about which traits [are] to be included in the breeding objective should be based on purely economic grounds, and not on whether they are difficult or easy to measure or to change genetically (Ponzoni and Newman 1989)." Accordingly, a breeding objective should account for all inputs (e.g. establishment costs, management costs, harvesting costs, transport costs and processing costs) and outputs (e.g. income from the sale of sawn boards and pulpwood) in a production system (Ponzoni and Newman 1989; Borralho *et al.* 1993). In practice, consideration is generally given to availability of genetic and economic information when defining objective traits (Borralho *et al.* 1993).

1.4.3 Sawn-timber breeding objectives

Extensive production system modelling has been undertaken for pulpwood production (Borralho *et al.* 1993; Greaves *et al.* 1997a). These studies identified volume, basic density and pulp yield at rotation age as the most economically important pulpwood objective traits based on monetary cost savings per tonne of pulp produced.

The definition of a formal *E. globulus* and *E. nitens* sawn-timber breeding objective and the estimation of economic weights for objective traits is more complex than for pulpwood because (1) solidwood plantation growers usually produce a range of products with different ideal wood properties and different values from the same trees (i.e. both the value of products and the costs of their production can vary substantially with changes in biological traits) and (2) as yet there are no strong 'market signals' to forest growers because the industry is 'young' and markets for this timber are not well established (Raymond 2000; Greaves *et al.* 2004a; Kube and Raymond 2005).

If *E. globulus* and *E. nitens* are to be grown on a large scale for the production of appearance-grade sawn timber, reducing the economic impact of drying degrade will be an important objective for growers, processors and researchers into the foreseeable future. Little is known about the genetics of drying degrade in *E. nitens*

and *E. globulus* (Kube and Raymond 2005). However, given the lack of wholly effective technological and/or silvicultural solutions, the study of genetic variation in drying degrade traits and the possibility of breeding for improvement in these traits are key research priorities and the principal focus of this thesis. Furthermore, if thinning and sawing residues are to be sold as pulpwood, sawn-timber breeding objectives for *E. globulus* and *E. nitens* are likely to include pulpwood objective traits (Greaves and McRae 2004).

1.4.4 Improving objective traits

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'Breeding objective' traits can be improved by implementing new processing technologies (e.g. adopting controlled kiln-drying and reconditioning to minimise drying degrade), modifying silviculture (e.g. early thinning to maximise log diameters and pruning to minimise knots) or breeding. If breeding is to be used as a tool to improve an objective trait:

- there must be exploitable genetic variation in the objective trait (i.e. it must be heritable) that is expressed in a stable manner across the targeted plantation region (i.e. minimal expression of genotype by environment interaction; refer to Wu and Matheson 2005),
- it must be inexpensive to estimate the genotypic value of trees in terms of the objective trait, and
- it should be cheaper than, augment or be more effective than modifying technology and/or silviculture.

1.4.4.1 Exploitable genetic variation in E. globulus and E. nitens

Genetic variation between populations

Genetic variation in natural stands of *E. globulus* and *E. nitens* can be partitioned into among-population genetic variation and within-population genetic variation. However, there are a number of levels of 'population' among and within which genetic variation can be examined and/or exploited for genetic gain (e.g. localities within subraces and subraces within races; Dutkowski and Potts 1999; Dutkowski *et al.* 2001). The identification of such geographically and genetically distinct native forest populations can increase genetic gain by enabling the selection of the best native forest populations for inclusion in breeding populations and/or

improving the prediction of breeding values for trees within established breeding populations (Quaas 1988; Dutkowski and Potts 1999; Dutkowski *et al.* 2001).

Genetic variation within populations

Non-additive genetic variation

Within populations, genetic variation can be further partitioned into additive and non-additive genetic variation (Falconer 1986). Non-additive genetic variation can be fully exploited by breeders and plantation growers if clones (i.e. clonal forestry) can be deployed into plantations and partially exploited if full-sib families (i.e. family forestry) can be deployed (Costa e Silva *et al.* 2004). Currently, neither of these options is practiced commercially in *E. nitens*. *Eucalyptus nitens* control-pollinated seed is expensive to produce and clonal propagation of the species is notoriously difficult (Maile and Nieuwenhuis 1995; Williams *et al.* 1999; Moncur and Boland 2000). The marginal economic value of genetic gains achieved through the exploitation of non-additive genetic variation is not currently considered sufficient to outweigh the associated higher deployment costs, especially in the case of short-rotation pulpwood plantations (Borralho 1997). In contrast, control-pollinated (CP) family, mass supplementary pollinated (MSP) family and clonal deployment strategies are practiced by *E. globulus* growers (Griffin 2001; Araújo *et al.* 2004; Patterson *et al.* 2004).

Additive genetic variation

Additive genetic variance is the variance of true breeding values (Falconer 1986). The true breeding value (i.e. additive genetic value) of an individual tree is twice the mean deviation of that tree's progeny from the population trait mean, assuming that tree was mated to a large number of individuals taken at random from the population (Falconer 1986). True breeding values are never known but are estimated by breeders through the analysis of data from progeny trials. Most analyses of *E. globulus* and *E. nitens* progeny trials currently utilise mixed models to account for fixed effects, spatial relationships and genetic relationships among observations in the calculation of best linear unbiased predictions (BLUPs) of breeding values (Borralho 1995; Mrode 1996; Dutkowski *et al.* 2002). In such analyses, variance and covariance parameters (including additive genetic variance components and

additive genetic covariances/correlations) are usually estimated using restricted maximum likelihood (REML) procedures (Gilmour *et al.* 2002).

Additive genetic correlation

Correlations between breeding values are additive genetic correlations. Tree breeders use genetic correlations to account for additive genetic relationships among assessment ages, traits and sites. Three types of genetic correlation are commonly identified:

- interage genetic correlations are used to "predict response at harvest to selection carried out in young trees (Williams *et al.* 2002)"
- intertrait genetic correlations are used to predict response in one trait (e.g. an objective trait) from selection for another trait (e.g. a selection trait, refer to Section 1.4.4.2; Borralho 1995; Williams *et al.* 2002)
- intersite genetic correlations are used to "predict response to selection at one site when selecting at another (Williams *et al.* 2002)" The less the genotype by environment interaction, the higher the intersite genetic correlation (Burdon 1977).

Multivariate models incorporating interage, intertrait and intersite correlations are used in the analysis of progeny trial data to increase the precision of breeding value estimates and thus maximise additive genetic gains from selection (Henderson 1984; Henderson 1986).

1.4.4.2 Selection traits

In reality objective traits are rarely assessed in tree breeding programmes because they cannot be assessed until rotation age, require trees to be felled, are inherently expensive to assess and/or are difficult to measure. Instead selection traits are assessed on trees in progeny trials and selection trait breeding values are estimated (Ponzoni and Newman 1989). Estimated breeding values for objective traits can be calculated from the estimated breeding values of selection traits if additive genetic covariances (or correlations) between objective and selection traits and additive genetic covariances among selection traits are known or assumed (Borralho 1995). Preferably selection traits should be non-destructive, inexpensive to assess and strongly genetically correlated with objective traits (Raymond and Apiolaza 2004).

1.5 Aims of this thesis

The principal aims of this thesis were to:

- collate existing information and identify gaps in knowledge relating to genetic variation in *E. nitens* (Chapter 2).
- present standard estimates of *E. nitens* genetic parameters (Chapter 2).
- examine genetic variation in, intertrait correlations among and practical aspects of different methods of wood sample shrinkage assessment (Chapters 3 and 5).
- examine intertrait correlations among wood sample shrinkage and pulpwood selection traits (Chapters 3 to 7).
- examine intersite correlations in wood sample shrinkage traits and pulpwood selection traits (Chapters 3 and 4).
- examine correlations in wood sample shrinkage traits among drying treatments (Chapter 5).
- examine intertrait correlations between pulpwood and solidwood 'selection traits' and 'objective traits' (Chapter 6).
- examine genotype by height interaction in pulpwood and solidwood traits (Chapter 7).

CHAPTER 2

2. A REVIEW OF GENETIC PARAMETERS AND VARIATION IN *EUCALYPTUS NITENS*

2.1 Introduction

The objectives of this review were to (1) collate information relating to genetic variation among and within *E. nitens* populations, (2) present standard estimates of genetic parameters within populations (i.e. coefficients of additive genetic variation, heritabilities, additive genetic correlations and phenotypic correlations) for as many growth, wood property, tree architecture and fitness traits as possible, and (3) identify areas or traits in which further research is required.

2.2 Genetic Variation in *E. nitens*

2.2.1 Eucalyptus nitens: one species or two?

Pederick (1977; 1979) and Pederick and Lennox (1979) identified two forms of *E. nitens* and considered these forms sufficiently distinct to recognise them as different varieties, *E. nitens* var. *nitens* and var. *errinundra*. Pederick (1979) noted that trees of the Errinundra type "are characterised by relatively slow growth, narrow, weakly glaucous juvenile leaves, which with their stems are often coloured pink during winter and spring, a change to adult foliage commencing about one year after planting [c.f. two to four years], adult leaves with slightly denticulate margins and with the gland-like structures, and the absence of the highly fluorescent polyphenol [i.e. stilbene] in the [adult and juvenile] foliage." Some plants from central Victoria were observed to resemble those from the Errinundra region (Figure 2.1).

AUTHOR'S NOTE (14 December 2011)

Data from Chapter 2 are reported in the following peer-reviewed papers:

Hamilton MG, Potts BM (2008) Review of *Eucalyptus nitens* genetic parameters. *New Zealand Journal of Forestry Science* **38**, 102–119. http://eprints.utas.edu.au/7290/

Hamilton M, Joyce K, Williams D, Dutkowski G, Potts B (2008) Achievements in forest tree improvement in Australian and New Zealand. 9. Genetic improvement of *Eucalyptus nitens* in Australia. *Australian Forestry* **71**, 82-93. http://eprints.utas.edu.au/6788/

Hamilton MG, Dutkowski GW, Joyce KR, Potts BM (2011) Meta-analysis of racial variation in *Eucalyptus nitens* and *E. denticulata*. *New Zealand Journal of Forestry Science* **41**, 217-230. http://eprints.utas.edu.au/12425/

A meta-analysis of Pederick provenance variation in *Eucalyptus nitens* and *E. denticulata* is reported in:

Hamilton MG, Potts BM (2005) 'A review of genetic parameters and variation in *Eucalyptus nitens* (shining gum).' Cooperative Research Centre for Sustainable Production Forestry, Technical Report 158, Hobart, Tasmania.

CHAPTER 3

3. THE EFFECT OF ASSESSMENT METHOD ON THE EXPRESSION OF GENETIC VARIATION IN GROSS SHRINKAGE IN *EUCALYPTUS NITENS* WOOD CORES

3.1 Introduction

Large areas of *E. nitens* plantation have been established in temperate regions of the southern hemisphere, particularly in Australia (c. 160,000 ha in 2004) and Chile (c. 140,000 ha in 2004; INFOR 2004a). Although kraft pulpwood production is the principal focus of most *E. nitens* growers, there is increasing interest in producing sawn-timber from plantations (Neilsen and Pinkard 2000; FEA 2004; Gunns 2004; INFOR 2004c; Kube and Raymond 2005; Nolan *et al.* 2005).

Volume, basic density and pulp yield at rotation age have been identified as the most economically important breeding objective traits for kraft pulpwood production (Borralho *et al.* 1993; Greaves *et al.* 1997a). However, defining equivalent traits for sawn-timber is more complex because solidwood plantation growers usually produce a range of products with different monetary values and different ideal wood properties (e.g. pulpwood and sawn boards). Furthermore, the market values of plantation-grown solidwood products are not easily determined (Raymond 2000; Greaves *et al.* 2004a; Kube and Raymond 2005). However, given that pulpwood is a valuable by-product of sawmilling and both high growth and basic density are desirable properties for sawn-timber production (AS/NZS 2878 2000; Raymond 2000; Greaves *et al.* 2004c), these traits are likely to be included in sawn-timber breeding objectives (Greaves *et al.* 2004a).

Reducing the impact of drying degrade is also likely to be an objective of sawn-timber breeding programmes. Drying defects, such as cupping, face checking (i.e. exposed cracks), internal checking, splitting and washboarding (i.e. corrugations on the face of boards) are caused by within-board variation in shrinkage (Kauman 1964a; Bootle 1983; Chafe 1992; Vermaas 1995; Svensson and Martensson 1999; Taylor *et al.* 2003; Nolan *et al.* 2005). Some sawmilling studies have concluded that drying degrade can be managed effectively with the adoption of appropriate sawmilling and drying strategies (Waugh and Yang 1994; Washusen 2001) but most have indicated that drying degrade will substantially reduce the

AUTHOR'S NOTE (14 December 2011)

Data from Chapter 3 are reported in the following conference paper and poster:

Hamilton MG, Potts BM, Harwood CE, Apiolaza L, Gore P (2004) Comparison of non-destructive assessment techniques for shrinkage and collapse in *Eucalyptus nitens*. In '*Eucalyptus* in a changing world. Proceedings of an IUFRO conference'. Aveiro, Portugal. (Eds N Borralho, JS Pereira, C Marques, J Coutinho, M Madeira and M Tomé) pp. 686-687. (RAIZ). http://eprints.utas.edu.au/6660/

CHAPTER 4

4. GENETIC VARIATION IN VOLUME-ASSESSED COLLAPSE, NET SHRINKAGE AND GROSS SHRINKAGE IN *EUCALYPTUS NITENS* WOOD CORES

4.1 Introduction

Eucalyptus nitens pulpwood breeders generally select trees according to diameter at breast height and wood core basic density (or pilodyn penetration) at a young age, based on the assumption that these non-destructive and cheaply-assessed 'selection traits' are strongly genetically correlated with the 'objective traits' of rotation-age volume and basic density (Ponzoni and Newman 1989; Borralho 1995; Raymond and Apiolaza 2004). More recently, cellulose content predicted using near infrared reflectance (NIR) analysis has shown promise as a cheap and non-destructive means of selecting trees for high pulp yield (Schimleck *et al.* 1997; Raymond and Schimleck 2002; Schimleck *et al.* 2004). The correlation between pulp-yield and cellulose content has been shown to be positive and strong in several studies (Wallis *et al.* 1996a; Wallis *et al.* 1996b; Kube and Raymond 2002a). Further to pulpwood selection traits, the measurement of shrinkage in 12 mm wood cores is one assessment technique proposed as a cheap and non-destructive means of identifying genotypes with low susceptibility to drying defects in sawn timber (Kube and Raymond 2001; Hamilton *et al.* 2004a; McConnochie *et al.* 2004; Chapter 3; Raymond *et al.* 2004).

The principal aims of this *E. nitens* study were to examine (1) differences between sites in, (2) subrace and additive genetic variation in, (3) genetic correlations among and (4) intersite correlations for diameter at breast height, basic density, NIR predicted cellulose content and shrinkage properties (volume-assessed gross shrinkage, net shrinkage and recoverable collapse).

AUTHOR'S NOTE (14 December 2011)

Data from Chapter 4 are reported in the following peer-reviewed paper:

Hamilton MG, Raymond CA, Harwood CE, Potts BM (2009) Genetic variation in *Eucalyptus nitens* pulpwood and wood shrinkage traits. *Tree Genetics and Genomes* **5**, 307-316. http://eprints.utas.edu.au/7289/

CHAPTER 5

5. THE EFFECTS OF DRYING TEMPERATURE AND METHOD OF ASSESSMENT ON THE EXPRESSION OF GENETIC VARIATION IN GROSS SHRINKAGE IN *EUCALYPTUS GLOBULUS* WOOD SAMPLES

5.1 Introduction

Large areas of *E. globulus* plantation have been established for the production of pulpwood in Australia, Chile, Portugal and Spain (Potts *et al.* 2004). Volume, basic density and pulp yield at rotation age have been identified as the most economically important breeding objective traits for kraft pulpwood production (Borralho *et al.* 1993; Greaves *et al.* 1997a). Pulpwood breeders aim to improve these 'objective traits' by selecting trees according to non-destructive and cheaply-assessed 'selection traits' (e.g. diameter at breast height and wood core basic density) based on the assumption that genetic correlations between objective and selection traits are strong (Ponzoni and Newman 1989; Borralho 1995; Raymond and Apiolaza 2004).

Although pulpwood production is the principal focus of most *E. globulus* growers, there is increasing interest in using plantation-grown *E. globulus* to produce solidwood products. Sawmilling studies have shown that adequate recoveries of dried appearance-grade products are possible from *E. globulus* grown in appropriately managed plantations (Waugh and Yang 1994; Moore *et al.* 1996; Nutto and Vazquez 2004; Washusen 2004; Waugh 2004). However, increasing product value by reducing drying degrade is likely to be an objective of sawn-timber breeders (Raymond 2000; Greaves *et al.* 2004a). The presence of drying defects such as cupping, face checking (i.e. exposed cracks) and internal checking can cause degrade in, and reduce the value of, appearance-grade sawn timber (Washusen *et al.* 2000a; Nutto and Vazquez 2004; Waugh 2004; Nolan *et al.* 2005).

If breeding for reduced drying degrade is to be practical and cost effective, suitable low-cost and non-destructive methods of identifying genotypes that are superior in these traits are required. The measurement of gross shrinkage in wood samples, such as 12 mm cores, is one proposed means of identifying such genotypes (Kube and Raymond 2001; Hamilton *et al.* 2004a; Chapters 3 and 4). Gross shrinkage is composed of normal shrinkage, recoverable collapse and non-recoverable collapse

AUTHOR'S NOTE (14 December 2011)

Data from Chapter 5 are reported in the following peer-reviewed paper:

Hamilton MG, Harwood CE, Potts BM (2009) The effects of drying temperature and method of assessment on the expression of genetic variation in gross shrinkage of *Eucalyptus globulus* wood samples. *Silvae Genetica* **58**, 252-261. http://eprints.utas.edu.au/9685/

CHAPTER 6

6. SELECTION TRAITS, WHOLE-TREE VALUES AND BREEDING OBJECTIVE TRAITS IN *EUCALYPTUS GLOBULUS*

6.1 Introduction

As outlined in Chapter 5, increasing product value by reducing drying degrade is likely to be an objective of *E. globulus* sawn-timber breeders (Raymond 2000; Greaves *et al.* 2004a). Drying defects such as cupping, face checking and internal checking can reduce the value of appearance-grade sawn timber (Washusen *et al.* 2000a; Nutto and Vazquez 2004; Waugh 2004; Nolan *et al.* 2005). Resistance to indentation, measured as Janka hardness, is another important characteristic in some solidwood applications (e.g. flooring; Bootle 1983; AS 2796.1 1999; Nolan *et al.* 2005) that might also be improved through breeding.

If breeding for reduced drying degrade or improved hardness is to be practical and cost effective, non-destructive and cheap methods of identifying genotypes that are superior in these traits are required. Checking in discs (McKenzie *et al.* 2003a; McConnochie *et al.* 2004), the properties of board ends (Yang and Fife 2003) and Silviscan™-assessed traits (McKenzie *et al.* 2003a) have been shown to be strongly phenotypically correlated with board properties in temperate eucalypts. However, the extraction of discs and/or board ends requires trees to be felled and Silviscan™ is too expensive for use in operational breeding. The measurement of shrinkage in small wood samples, such as 12 mm cores, is one proposed non-destructive and low-cost means of identifying superior solidwood genotypes (Kube and Raymond 2001; Hamilton *et al.* 2004a; McConnochie *et al.* 2004; Chapters 3 to 5).

The aims of this study were to quantify phenotypic and genetic variation in, and correlations between, both currently utilised pulpwood and proposed solidwood selection traits (i.e. DBH, sample basic density and sample gross shrinkage) and objective traits (i.e. whole-tree volume, whole-tree basic density, board hardness, board cupping and board checking) in *E. globulus*.

AUTHOR'S NOTE (14 December 2011)

Data from Chapter 6 are reported in the following peer-reviewed paper:

Hamilton M, Potts B, Greaves B, Dutkowski G (2010) Genetic correlations between pulpwood and solidwood selection and objective traits in *Eucalyptus globulus*. *Annals of Forest Science* **67**, Article 511. http://eprints.utas.edu.au/9835/

CHAPTER 7

7. PATTERNS OF LONGITUDINAL WITHIN-TREE VARIATION IN PULPWOOD AND SOLIDWOOD TRAITS DIFFER AMONG *EUCALYPTUS GLOBULUS* GENOTYPES

A manuscript based on this chapter has been submitted for publication in Annals of Forest Science and is currently in review.

7.1 Introduction

For breeding and mensurational purposes it is desirable to estimate whole-tree wood quality values for commercially important traits using cheap and non-destructive sampling techniques (Raymond *et al.* 1998). Knowledge of within-tree variation is required to determine the most representative point to sample or measure and to develop relationships between point estimates and whole-tree values (Raymond and MacDonald 1998; Igartua *et al.* 2003). Mensurationists also use knowledge of longitudinal within-tree variation to estimate yields of individual product classes (e.g. log sizes by diameter and length; Newnham 1988). Similarly, timber processors can use such knowledge to ensure trees are used in the most appropriate and profitable manner by modifying processing practices or allocating logs to particular end uses according to the known properties of different stem sections.

Patterns of longitudinal variation in traits may differ among genotypes. Such genotype by height category interaction may introduce bias according to genotype in estimates of whole-tree values (e.g. Guimaraes *et al.* 1995) and/or the characteristics of specific sections of the stem derived from sample measurements.

This study examines longitudinal variation in diameter under bark, bark thickness, basic density, kino, decay and shrinkage properties of *E. globulus*. Furthermore, it investigates whether patterns of longitudinal variation are consistent across subraces and families within subraces. Differences among genotypes are discussed in this context.

AUTHOR'S NOTE (14 December 2011)

Data from Chapter 7 are reported in the following peer-reviewed paper:

Hamilton MG, Greaves BL, Potts BM, Dutkowski GW (2007) Patterns of longitudinal within-tree variation in pulpwood and solidwood traits differ among *Eucalyptus globulus* genotypes. *Annals of Forest Science* **64**, 831–837. http://eprints.utas.edu.au/3393/

CHAPTER 8

8. GENERAL DISCUSSION AND CONCLUSION

8.1 Introduction

Although pulpwood production is the principal focus of most *Eucalyptus globulus* and *E. nitens* forest growers, there is increasing interest in producing sawn-timber from plantations (Neilsen and Pinkard 2000; McKenzie *et al.* 2003b; Bermúdez *et al.* 2004; FEA 2004; Gunns 2004; INFOR 2004b; McConnochie *et al.* 2004; Nutto and Vazquez 2004; Waugh 2004; Kube 2005b; Nolan *et al.* 2005). This thesis examined breeding as a means of improving the pulpwood and solidwood characteristics of *E. globulus* and *E. nitens*.

Eucalyptus nitens pulpwood breeders generally select trees according to diameter at breast height and wood core basic density (or pilodyn penetration) at a young age, based on the assumption that these non-destructive and cheaply-assessed 'selection traits' are strongly genetically correlated with the 'objective traits' of rotation-age whole-tree volume and basic density (Ponzoni and Newman 1989; Borralho 1995; Raymond and Apiolaza 2004). More recently, cellulose content predicted using near infrared reflectance (NIR) analysis has shown promise as a cheap and non-destructive means of selecting trees for high pulp yield (Schimleck *et al.* 1997; Raymond and Schimleck 2002; Schimleck *et al.* 2004).

Given that pulpwood is a valuable by-product of sawmilling and that traits such as rapid growth and high basic density are desirable for both pulpwood and sawn timber production (AS/NZS 2878 2000; Raymond 2000; Greaves *et al.* 2004c), these traits are also likely to be included in sawn-timber breeding objectives (Greaves *et al.* 2004a). Further to examining genetic variation in and genetic relationships among 'pulpwood' selection traits, this thesis investigated the utility of measuring shrinkage in wood samples (e.g. 12-mm cores), extracted for the measurement of basic density and/or cellulose content, as a cheap and non-destructive means of selecting against drying defects in sawn products. Genetic and within-tree longitudinal variation in other traits (e.g. bark thickness, kino, decay) were also examined.

8.2 Genetic control of pulpwood and solidwood selection traits

8.2.1 Between populations

In this thesis the analysis of genetic variation in traits was partitioned into among-population (e.g. among-subrace) and within-population genetic variation (Chapters 1 and 2). In two *E. nitens* progeny trials (Meunna and Tarraleah; Chapter 4) the Southern subrace generally exhibited better qualities than the Northern and Connor's Plains subraces for kraft pulpwood and most solidwood applications in most traits: it exhibited the greatest diameter, highest basic density (although differences between subraces were not significant), greatest predicted cellulose content, least gross shrinkage (at Meunna but not Tarraleah, although differences between subraces were not significant at either site) and least collapse. However, meta-analysis of previously published data found that Connor's Plain had a greater diameter than Southern and Northern subraces on most winter rainfall sites (Chapter 2). This inconsistency was possibly caused by genotype by environment interaction or the mistaken identification of *E. denticulata* genotypes as *E. nitens* in some early trials.

Significant differences among ten *E. globulus* subraces were observed in diameter, sample basic density and sample gross shrinkage (Chapter 5). The relative performances of subraces for diameter and basic density in this study were broadly consistent with previously published results (Dutkowski and Potts 1999; Muneri and Raymond 2000; Lopez *et al.* 2001).

8.2.2 Within populations

8.2.2.1 Genetic control of pulpwood selection traits

Diameter and sample basic density were found to be under moderate to strong genetic control within populations and within the range of previous estimates in *E. nitens* (Chapter 2) and *E. globulus* (Volker *et al.* 1990; MacDonald *et al.* 1997; Muneri and Raymond 2000; Raymond *et al.* 2001; Lopez *et al.* 2002) in most of the trials studied (Chapters 3 to 6). However, an atypically low heritability estimate for diameter was found in one *E. nitens* trial (Magazine Road; Chapter 3) probably due to variable browsing pressure, soil compaction and weed control and the relatively young age of assessment.

In *E. nitens* cellulose content was under strong additive genetic control at both of the sites analysed for this trait (Meunna and Tarraleah; Chapter 4). However, predicted genetic gains through phenotypic selection within subraces were particularly small, reflecting the relatively low level of phenotypic variation in cellulose content.

8.2.2.2 Genetic control of shrinkage traits

Calliper-assessed and visually-ranked sample gross shrinkage exhibited significant additive genetic variation and were under moderate to strong genetic control in all of the trials in which these traits were assessed (Chapters 3 and 5). Although additive genetic variance in volume-assessed gross shrinkage was also significant in *E. nitens* trials (Chapters 3 and 4), a larger scale study is required to definitively determine the extent to which this trait is under additive genetic control in *E. globulus* (refer to Chapter 5).

In contrast with volume-assessed gross shrinkage, which was a composite measure of gross shrinkage in all axes (i.e. tangential, radial and longitudinal), calliper-assessed and visually-ranked gross shrinkage were both measures of tangential gross shrinkage. However, strong genetic correlations were observed between pair-wise combinations of the three assessment techniques implying that they could be used interchangeably in breeding programmes. Accordingly, practical consideration should determine which of these techniques is used to assess gross shrinkage (Chapters 3 and 5).

Of those gross shrinkage measurement techniques identified as possible selection traits according to genetic criteria (i.e. calliper-assessed, volume-assessed and visually-ranked gross shrinkage) none required specialised skills or equipment and all required only one additional measurement in addition to that required to assess basic density. However, the assessment of volume had some practical advantages over other measurement techniques. Volume-assessment was the most rapid technique if gross shrinkage was not visibly obvious in samples (e.g. in those dried under mild conditions), as it was not necessary to rank samples or identify points of maximum shrinkage within them. Furthermore, the visual-ranking technique would not allow comparison of shrinkage across generations, sites or ages.

Radial gross shrinkage (Chapter 5) and a four-point visual score of sample tangential gross shrinkage (Chapter 3) are unlikely to be useful selection traits, because they did not exhibit significant additive genetic variance (Chapters 3 and 5). Although additive genetic variation was found in gross shrinkage at one of two sites assessed (George's Plains and Magazine Road) using image analysis, the expected genetic gain through phenotypic selection using this assessment technique was very low (Chapter 3).

8.2.2.3 Intertrait correlations among shrinkage selection traits

Components of gross shrinkage (i.e. recoverable collapse and net shrinkage) were examined separately in two *E. nitens* trials (Meunna and Tarraleah; Chapter 4). Even though net shrinkage comprised a larger proportion of gross shrinkage than collapse, the genetic correlation between gross shrinkage and collapse was very strong and positive indicating that gross shrinkage could be used to effectively select against core collapse at less expense than direct measurement. However, if gross shrinkage is to be used as a proxy for recoverable collapse, samples should be dried relatively rapidly from the green condition (i.e. at high temperature and/or low humidity) to exacerbate the expression of collapse.

In *E. globulus* strongly positive subrace and genetic correlations in gross shrinkage among three drying treatments (22°C, 60°C and 105°C) indicated that the rankings of genotypes were very similar across drying treatments (i.e. there was no evidence of genotype by drying treatment interaction). Accordingly, these drying treatments could be used interchangeably in breeding programmes (Chapter 5) according to the requirements of other selection traits (e.g. basic density or cellulose content).

8.3 Intersite correlations in selection traits

8.3.1 Pulpwood traits

Intersite genetic correlations were examined in *E. nitens* (Chapters 2 to 4). On a broad scale, meta-analysis of data compiled from the literature revealed significant subrace by rainfall zone interaction in growth traits. In general, in areas with predominantly summer rainfall (e.g. southern Africa and NSW) NSW populations

grew most rapidly and in areas with predominantly winter rainfall (e.g. Tasmania and Chile) central Victorian populations grew most rapidly.

The intersite additive genetic correlation for diameter was weak and not significantly different to zero in one study of two Tasmanian *E. nitens* trials (George's Plains and Magazine Road; Chapter 3). However, trial establishment effects and the young age of assessment, rather than an underlying genotype by environment interaction, may have caused this low genetic correlation. In another study across two trials (Meunna and Tarraleah; Chapter 4), intersite genetic correlation for diameter was strong. Intersite genetic correlations for basic density and cellulose content were also found to be strong in both *E. nitens* studies (Chapters 3 and 4), reflecting the strong genetic control of these traits.

8.3.2 Shrinkage traits

Intersite genetic correlations for shrinkage traits were variable in *E. nitens*. In the George's Plains/Magazine Road study (Chapter 3), intersite correlation for volume-assessed gross shrinkage was strong. In contrast, the equivalent correlation in the Meunna/Tarraleah study (Chapter 4) was weak, as was the intersite correlation for recoverable collapse. However, as the Meunna trial had been thinned 3 years prior to assessment and Tarraleah had not, these weak intersite correlations may have been caused by genotype by environment interaction and/or genotype by silviculture interaction. Further research is required to elucidate the effect of silviculture and/or environment on the genetic expression of collapse and the practical implications of any such interactions for breeding programmes.

8.4 Intertrait correlations among selection traits

8.4.1 Intertrait correlations among pulpwood selection traits

Subrace correlations in *E. globulus* (Chapter 5) and within subrace additive genetic correlations in both *E. nitens* and *E. globulus* (Chapters 3 to 5) between diameter and sample basic density were generally found to be weak, negative (i.e. adverse) and not significantly different to zero. In contrast, the genetic correlations of cellulose content with DBH and basic density were observed to be positive (i.e. favourable) in a study of *E. nitens* (Chapter 4). These findings were consistent

with the findings of Tibbits and Hodge (1998), but not wholly consistent with those of Kube and Raymond (2001) who found the genetic correlation between cellulose content and basic density to be negative. Further research is required to clarify the direction and strength of correlations between cellulose content and other pulpwood selection traits.

8.4.2 Intertrait correlations between sample shrinkage and pulpwood traits

Although estimated phenotypic correlations between diameter over bark and gross shrinkage in both *E. nitens* and *E. globulus* were adverse (i.e. gross shrinkage increased with diameter, Chapters 3 to 5) and generally significantly different to zero, further studies are required to definitively elucidate the relationship between these traits at the subrace and additive genetic level. Previous estimates of the genetic correlation between calliper-assessed gross shrinkage and diameter in *E. nitens* (Kube and Raymond 2005) were stronger than those observed in this thesis.

In most *E. nitens* and *E. globulus* trials, a negative (i.e. favourable) correlation between basic density and gross shrinkage was observed at the subrace, genetic and phenotypic level (Chapters 3 to 5). These strong negative genetic correlations were consistent with previous findings in eucalypts (Ilic 1999; Kube and Raymond 2001; Arnold *et al.* 2004) and the theoretical basis of collapse (Chafe 1992). They indicated that selection for higher basic density would result in a favourable correlated response in gross shrinkage. In *E. nitens* genetic correlations between cellulose content and collapse and cellulose content and gross shrinkage were not significantly different to zero (Chapter 4). However, a positive genetic correlation between cellulose content and net shrinkage was observed, despite a lack of significant genetic variance in net shrinkage.

8.5 Genetic variation in objective traits and correlations between selection traits and objective traits

The findings of a study examining the relationship between selection traits and objective traits in *E. globulus* (Chapter 6) generally supported the assumptions underlying the use of diameter and core basic density as selection traits in pulpwood breeding programmes (i.e. significant genetic variance in selection and objective

traits, strong genetic correlation between selection and objective traits and strong interage genetic correlations). However, there was some evidence to suggest that subrace selection should be undertaken more than four years after planting. A weak subrace correlation was observed between DBH assessed at age four and whole-tree volume assessed at age 15. The findings of this study also indicated that selection for higher basic density and less gross shrinkage in wood samples would result in a correlated increase in Janka hardness in sawn boards. However, a larger scale study undertaken on a trial managed for solid wood production is required to definitively determine the effectiveness of selecting trees for reduced drying degrade according to cheaply-assessed and non-destructive selection traits. While positive and significant phenotypic correlations between selection traits and board drying-degrade traits were observed, corresponding subrace and genetic correlations were generally positive but not significantly different to zero.

8.6 Longitudinal within-stem variation and genotype by height interaction in pulpwood and solidwood traits

A study of longitudinal within-tree variation in *E. globulus* found the lower stem to have the least favourable wood properties for kraft pulpwood and most solidwood applications: bark was relatively thicker, basic density was lowest and kino, decay and shrinkage angle were greatest at or below 12% of tree height (Chapter 7). These longitudinal trends have adverse implications for forest managers and wood processors given that the lower stem represents a high proportion of total stem volume, is pruned at substantial expense under some solidwood silvicultural regimes and produces logs of the greatest diameter.

In this same study, high decay was observed at breast height in trees that had previously been sampled for physical and chemical properties. Accordingly, trees should be sampled for these properties on only one occasion to avoid the presence of excessive decay in samples. There was some evidence that the Southern Tasmania subrace was less effective than other subraces in restricting the spread of decay up the stem from breast height.

Evidence of subrace by height category interaction was identified in bark thickness, basic density, decay and gross shrinkage angle indicating that patterns of longitudinal variation in these traits differed among subraces.

8.7 Concluding remarks

This thesis contributes to the expanding body of knowledge relating to the genetic improvement of *E. globulus* and *E. nitens* for solidwood production. Existing information pertaining to genetic variation among and within *E. nitens* populations was comprehensively reviewed and gaps in knowledge identified. Meta-analysis of available data provided standard estimates of *E. nitens* genetic parameters for growth, wood property, tree architecture and fitness traits.

Genetic variation in and intertrait correlations among wood shrinkage traits in *E. globulus* and *E. nitens* were examined in the experimental chapters of this thesis. A strong correlation between volume-assessed recoverable collapse and gross shrinkage was revealed in a study of *E. nitens* wood cores, indicating that gross shrinkage could be used to select against core collapse at lower cost than direct measurement. Of the methods examined, the volume- and calliper-assessment techniques were found to be the most suitable shrinkage property selection traits based on genetic and practical considerations. In addition, strong intertrait genetic correlations among these assessment techniques and among different sample drying treatments suggested that they could be used interchangeably in breeding programmes. Discouragingly, low intersite genetic correlations for sample gross shrinkage and collapse were observed in one *E. nitens* study and, while a small-scale *E. globulus* sawmilling study revealed significant phenotypic correlations between sample gross shrinkage and drying defects in boards, significant correlations were not detected at the genetic level. Furthermore, a study of longitudinal within-tree variation in *E. globulus* found the lower stem to have the least favourable wood properties for kraft pulpwood and most solidwood applications. This study also revealed evidence of subrace by height interaction in a number of solidwood and pulpwood traits.

Examination of genetic correlations for cellulose content with diameter and basic density in *E. nitens* added to the limited published information relating to the genetic relationships among these key pulpwood traits. Furthermore, the assumptions underlying the use of diameter and core basic density as selection traits in pulpwood breeding programmes were generally supported by the findings of an *E. globulus* study. Intertrait correlations between wood sample shrinkage traits and pulpwood

selection traits confirmed that there is a strong and favourable correlation between gross shrinkage and basic density in both *E. nitens* and *E. globulus*, a relationship which suggested alignment to some degree of pulpwood and solidwood breeding objectives.

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Note: Numbered citations in Tables 2.1 to 2.15 and Appendices refer to the numbers enclosed in square brackets at the end of relevant references.

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